Plant growth rates and seed size: a re-evaluation

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Abstract: Small-seeded plant species are often reported to have high relative growth rate or RGR. However, because RGR declines as plants grow larger, small-seeded species could achieve higher RGR simply by virtue of their small size. In contrast, size-standardized growth rate or SGR factors out these size effects. Differences in SGR can thus only be due to differences in morphology, allocation, or physiology. We used nonlinear regression to calculate SGR for comparison with RGR for 10 groups of species spanning a wide range of life forms. We found that RGR was negatively correlated with seed mass in nearly all groups, but the relationship between SGR and seed mass was highly variable. We conclude that small- seeded species only sometimes possess additional adaptations for rapid growth over and above their general size advantage.

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Running head: Seed size and growth rates

Abstract

Small-seeded species are often reported to have high relative growth rate or RGR. However, because RGR declines as plants grow larger, small-seeded species could achieve higher RGR simply by virtue of their small size. In contrast, size-standardized growth rate or SGR factors out these size effects. Differences in SGR can thus only be due to differences in morphology, allocation or physiology. We used non-linear regression to calculate SGR for comparison with RGR for ten groups of species spanning a wide range of life-forms. We found that RGR was negatively correlated with seed mass in nearly all groups, but the relationship between SGR and seed mass was highly variable. We conclude that small-seeded species only sometimes possess additional adaptations for rapid growth over and above their general size advantage.

Key words: RGR, SGR, life-history trade-offs, non-linear regression.

Introduction

A negative relationship between seed mass and seedling relative growth rate (RGR) has been documented in numerous plant groups (Maranon and Grubb 1993, Bloor and Grubb 2003, Rey et al. 2004, Paz et al. 2005, Baraloto and Forget 2007, Poorter et al. 2008) and is considered almost a truism in plant ecology. This relationship is commonly interpreted as part of the *r-K* continuum (Gadgil and Solbrig 1972, Kitajima and Myers 2008) – also called the disturbance-competitor axis (Paine and Levin 1981), the successional niche (Pacala and Rees 1998) or the ruderal-competitor axis (Grime 2002). At one end of this spectrum are pioneer species that take advantage of disturbance events or gaps, and at the other end are species that are slower to colonize and/or grow, but can win in competition over the long term (Pacala and Rees 1998, Kitajima and Myers 2008). Pioneer species are expected to have both small seeds and high growth rates; however, here we outline why growth rate comparisons can be misleading, and why the expected relationship between seed size and growth rate might differ according to habitat and the nature of competition.

RGR and individual seedling growth rates

The usual metric for measuring growth is relative growth rate (RGR):

$$RGR = \frac{\ln(M_2 / M_1)}{t_2 - t_1} \qquad \text{eqn 1}$$

where M_i is the mass of the plant at time t_i. RGR is a natural measure of growth efficiency that seems to factor out differences in initial size, so allowing fair comparison among species. Experiments to estimate RGR usually grow plants for a fixed period of time, and RGR is therefore calculated at a common age for all species. Such calculations are easy to perform, and, as only two harvests are required per species, a large number of species can be compared for relatively little time and effort. Where multiple harvests are available, RGR can also be

estimated as the slope of a linear regression of ln(mass) against time (Poorter and Garnier 1996).

However, these traditional methods for estimating RGR assume that plants grow exponentially throughout their lives, i.e. $M_t = M_0 e^{\beta t}$. In this case, RGR is given by β and differences in this parameter can only be due to differences in morphology, allocation and/or physiology. Thus, RGR can reasonably be thought of as a species trait (Grime and Hunt 1975, Shipley and Peters 1990, Hunt and Cornelissen 1997). RGR calculated in this way is a critical determinant of population growth rate in an empty habitat (i.e. one in which competition is minimal), and to see this, consider a population of n_t seeds of mass M_0. If all seeds germinate, the total mass of plants at the end of the growing season is $n_t M_0 e^{\beta T}$, where T is the length of the growing season. Assuming some fraction, *f*, of that plant mass is allocated to seed production, then the number of seeds in the next time interval is, $n_{t+1} = f n_t e^{\beta T}$, and the population growth rate (n_{t+1}/n_t) is therefore $f e^{\beta T}$, which is independent of seed mass (Figure 1A). Thus, seed mass would be a neutral trait (Turnbull et al. 2008b) and species could only increase their population growth rate – and hence exploit empty space more efficiently – by increasing β or by increasing the fraction of total mass converted to seeds (f).

In reality, however, plants cannot maintain exponential growth. Possible explanations for this include changes in allocation from productive to structural tissue and self-shading of the leaf canopy as plants get larger (Evans 1972, Maranon and Grubb 1993); the scaling of support and delivery networks (Enquist *et al.* 1999); and increasing resource limitation as plants grow larger (Ingestad and Agren 1992). So, for example, it is probably more realistic to assume that plant growth in the absence of competition follows a power-law ($dM/dt = \beta M^{\alpha}$ with $\alpha < 1$). In contrast to exponential growth, RGR now declines as plants grow larger (equation 5). This has important consequences for population growth. In this case (using equation 4) the number of seeds next year is given by:

$$n_{t+1} = f n_t \frac{\left(M_0^{1-\alpha} + (1-\alpha)\beta t\right)^{1/1-\alpha}}{M_0} \quad \text{eqn 2}$$

This leads to the simple conclusion that population growth rate (n_{t+1}/n_t) declines with seed mass, and over a realistic range of seed masses the effects are substantial (Figure 1B; although in reality other factors such as the scaling of *f* with plant size might reduce the steepness of this relationship). Thus, species can increase their population growth rate both by increasing β, but also by simply decreasing their seed size. Thus, seed size is no longer a neutral trait because species producing small seeds have an enormous population growth rate advantage in empty habitats even when all species follow the same growth curve (i.e. α and β are the same for all species).

Paradoxically, the RGR advantage accruing to small-seeded species means that they can actually reduce β without losing their population growth rate advantage. For example, we can re-run the simulation in Figure 1b but with β reduced by 5% for all species and see that this reduction has a relatively small effect compared to the effect of changing seed mass. Thus, in empty habitats, small-seeded species could maintain an RGR advantage over their larger-seeded counterparts while still investing in physiological adaptations that are known to be costly, such as frost tolerance (Agrawal *et al.* 2004) or herbivore defense (Bergelson and Purrington 1996; Koricheva 2002). Indeed, this investment may be more worthwhile for small-seeded species as small size is often associated with high seedling mortality (Rees and Venable 2007).

We now leave the case of empty habitats and instead consider individuals competing to capture vacant sites in a crowded environment; for example, tree seedlings competing for forest gaps (Dalling and Hubbell 2002). If a pioneer wants to win the race to the canopy, then it must be able to overtake and overtop its competitor; hence it must grow faster at a common size. We call this size-standardized measure of RGR, SGR, and have found it to be a better

predictor of the short-term outcome of competition in crowded environments than RGR (e.g. Fakheran *et al.* 2010). Hence, we might expect that pioneer species from competitive environments might have small seeds and high SGR, while those from open environments might have small seeds and low SGR.

Turnbull *et al*. 2008a showed that the relationship between RGR and seed size within a group of sand-dune annuals was negative while the relationship between SGR and seed size was positive. To investigate whether these two different growth metrics generally have different relationships with seed size, we here compare these relationships using ten different data sets each containing multiple species and incorporating a wide range of life-history strategies. We also investigate whether differences in the slopes of these relationships within studies can be explained by differences in life-form, co-occurrence or life-span which might reflect the different selection pressures experienced by different groups of species in different habitats.

Materials and methods

The ten studies are: A) a population of 31 recombinant inbred lines of *Arabidopsis thaliana* (Paul-Victor *et al.* 2010); B) nine European sand-dune annual species (Turnbull *et al.* 2008a); C) five European monocarpic species (unpublished data); D) seven European monocarpic species (Rose *et al.* 2009); E) nine west Asian annual grass species (unpublished data); F) eight European grass species including five perennials (unpublished data); G) nine European perennial grass species (Hautier *et al.* 2010); H) 21 C_3 and C_4 grass species including 18 perennials (Taylor *et al.* 2010); I) eight European herbaceous perennial species (unpublished data); J) six Bornean tree species from the family Dipterocarpaceae (unpublished data). For more details of all studies see Appendix 1. For the two monocarpic perennial data sets there was complete overlap among species; however, they are independent experiments carried out at different times. For the four grass data sets, there was very little species overlap (only one

species, *Dactylis glomerata* occurs in two data sets). Seed mass data was taken from the original studies and more details are provided in Appendix 1. The data sets were grouped in three different ways: 1) *by life-form*: forbs, grasses, trees; 2) *by co-occurrence*: whether or not the species represent a pool of naturally co-occurring species; 3) *by life-span*: whether the species are short- or long-lived. The typical life span of established plants in the short-lived category is less than 3-5 years; this group consists of annuals and short-lived monocarpic perennials; in the long-lived category typical life span of established plants is often greater than five years; this group consists of perennial grasses, forbs and trees. We used all studies for the life-form analysis, but only included the five perennial species from study F and the 18 perennial species from study H in order to have no studies with multiple life-form categories. Plants were usually started from seed (except study J where seedlings were used) and repeatedly measured (study D) or repeatedly harvested (all others). The experiments often incorporated additional treatments, e.g. high/medium/low light or different pot sizes. In this case, parameters are presented from one treatment only, always the one with the highest growth rate, e.g. the highest light level or the largest pot size.

Growth rate calculations

Conventional RGR was calculated using either 1) the average size of all individuals at the first and last available harvests (eqn 1); or 2) the slope of a linear regression between ln(size) and time. For comparison, we calculated SGR by fitting growth curves to plots of size versus time and calculating SGR at a common reference size (M_c); in this case, the average size of all plants halfway through the study (see also Rose *et al.* 2009, Paul-Victor *et al.* 2010, Hautier *et al.* 2010, Taylor *et al.* 2010, Paine *et al.* 2011). Calculating SGR involves fitting a growth curve using non-linear regression for each species to a plot of plant size (usually mass) versus time. SGR can be calculated at any size or simply plotted as a function of size; however, we used the average size halfway through the experiment to get a value of SGR that is

comparable to conventional RGR (which is also an average). The reference size obviously differs among studies, in keeping with the range of life-forms represented. Another advantage of choosing the average size halfway through each study is that, within a given study, all species occurred at the reference size during the lifetime of the experiments. Thus, we can calculate, for each species, the growth rate at M_c without extrapolating beyond the range of sizes observed for any species.

Fitting growth curves

Because of the nature of the data, we fitted different functional forms to different data sets. For all studies except one (sand-dune annuals – see Appendix 2) we fitted growth curves in R using either non-linear mixed-effects models where models required both fixed and random effects (*nlme*) or non-linear standard regression models where no random effect was required (*gnls*). When repeated measures were made on individuals, plant identity was included as the random effect (see Pinheiro and Bates 2000 for a description). In total we used four different growth functions, as appropriate for the different growth trajectories: power-law, asymptotic regression, asymptotic regression with an offset (von Bertalanffy), and the 4-parameter logistic. The choice of curve was determined by the nature of the data, in particular whether there was an indication of an asymptote, and refined by examining plots of residuals. All models were fitted with the help of a self-starting routine (with the exception of the power-law function) and following the general guidance laid out in Pinheiro and Bates (2000). For more detailed guidance on choosing a suitable growth curve and the mechanics of fitting such models see Paine *et al.* (2011). We illustrate the general method with an example below:

Power-law growth

It has been proposed that plant growth in an unrestricted setting should follow simple power laws (West *et al.* 2001). In this case the absolute growth rate can be written

$$\frac{dM}{dt} = \beta M^{\alpha} \qquad \text{eqn 3}$$

where β is an allometric constant, α is the scaling exponent and M is plant mass (or some other measure of size). Equation 3 has the following analytical solution:

$$M_t = \begin{cases} M_0 e^{\beta t} & \text{if } \alpha = 1 \\ (M_0^{1-\alpha} + (1-\alpha)\beta T)^{1/1-\alpha} & \text{if } \alpha \neq 1 \end{cases} \qquad \text{eqn 4}$$

where M_0 is the mass at $t = 0$, and this equation can be fitted directly to a plot of mass against time. The size-standardized instantaneous RGR, or SGR, is then given by

$$SGR = \frac{1}{M}\frac{dM}{dt} = \beta M_c^{(\alpha-1)} \qquad \text{eqn 5}$$

where M_c is the common reference mass. Power-law growth curves were fitted to studies where single individuals were grown in large pots (studies G, I and J) and there was little evidence of an approach toward an asymptote. Where mass was analyzed on the original scale, the variance was modeled as a power-function of the mean, using the function *varPower*. The remaining fitted functions first required log-transformation of the response variable (i.e. mass or size), but the same general principles apply.

Comparison of RGR and SGR

Once we had values of both RGR and SGR for each species we carried out an analysis of covariance and a mixed-effects model analysis (Pinheiro and Bates 2000) on the log-transformed growth rates. We used both types of analysis because statistical inference is simpler for analysis of covariance (Bolker *et al.* 2009), but this analysis does not allow us to partition the variance in slopes due to the grouping variables (e.g. life-form, co-occurrence and life-span). Average slopes were calculated from the analysis of covariance model using

contrasts. We carried out Spearman rank correlations on SGR and RGR values obtained from each study to see whether or not the rankings of species with respect to growth rate is affected by the choice of growth rate methodology.

Results

In the analysis of covariance there was a 3–way interaction ($F_{9,182} = 2.87$, $P < 0.003$; Fig 2) between growth metric (RGR vs. SGR), study, and ln(seed mass). As expected, the average slope of the relationship between ln(RGR) and ln(seed mass) was negative (average slope = –0.10, t = –4.39, df = 182, $P < 0.00002$) while the average slope between ln(SGR) and ln(seed mass) was non-significant (average slope = 0.035, t = 1.61, df = 182, $P > 0.10$).

In agreement with the analysis of covariance the mixed model analysis indicated the need for study-specific intercepts and slopes (random slopes and intercepts vs. random intercepts model: $x^2 = 18.01$; $P < 0.0002$). To try to understand why different studies required such different slopes we augmented the mixed model analysis with three different grouping variables: life-form did not affect the slope of the relationship between seed size and growth rate and neither did co-occurrence ($P > 0.05$ in both cases); however, there was a significant 3–way interaction between life-span (short-lived vs. long-lived), growth metric (SGR vs. RGR) and ln(seed mass) ($F_{1,20} = 10.35$, $P < 0.004$). The interaction occurred because the average slope of ln(SGR) vs. ln(seed mass) was positive for the short-lived species (average slope = 0.12, t = 3.85, df = 170, $P < 0.0002$) but negative (although non-significant) for the long-lived species (average slope = –0.045, t = –1.80, df = 170, $P > 0.07$).

Finally, Spearman rank correlations within each of the ten data sets revealed that RGR was correlated with SGR in only two studies, both of which were perennial grasses: study G ($\rho = 0.6$, $P = 0.048$, n = 9, 1–tailed test); and study H ($\rho = 0.42$, $P = 0.030$, n = 21, 1–tailed test). In the remaining eight data sets there was no significant positive correlation between

RGR and SGR. This indicates that in most studies, RGR cannot be used as a surrogate for a size-standardized growth rate.

Discussion

The overall slope of the relationship between conventional RGR and seed mass was strongly negative, supporting the idea that small-seeded species have a general RGR advantage due to their small size. In some ecological situations this advantage is biologically relevant, for example, giving small-seeded species higher population growth rates in an open environment where competition is minimal. This RGR advantage could therefore favor the evolution of small seeds in ruderal or pioneer species whose strategy is the rapid colonization of large areas of open habitat. However, this general RGR advantage that accrues solely through starting life at smaller size occurs without any additional physiological adaptations for rapid growth and needs to be separated from an SGR advantage. This is made clear in our analyses: while there was a general negative relationship between seed size and RGR across all groups, the slope of the seed size vs SGR relationship varied widely.

An SGR advantage occurs when plants grow faster at a given size. Among our ten datasets, positive relationships between seed size and SGR were particularly common among groups of short-lived species, for example among *Arabidopsis* genotypes, sand-dune annuals and monocarpic perennials. In three of these studies species with higher SGR were also found to have lower concentrations of defensive chemicals (study A; Paul-Victor *et al.* 2010, Zust et al. 2011), suffer more frost damage (study B; Turnbull *et al.* 2008a) or have a reduced capacity to tolerate simulated herbivory (study D; Rose *et al.* 2009). As explained in the introduction, this investment could arise because a small reduction in SGR is unlikely to negate the general RGR advantage of producing small seeds − and short-lived species often occur in open, disturbed habitats. It is also possible that the seed itself contributes enough nitrogen to the growing plant to induce a measurable growth rate advantage. In this case,

experiments conducted from seed would likely have different outcomes from those beginning with young plants or saplings.

An SGR advantage allows one individual to outgrow another in a competitive situation, such as might occur among saplings competing for canopy gaps. In our analysis negative relationships between SGR and seed size were commoner for long-lived plants, suggesting that in more competitive communities, small-seeded species have higher SGR. An SGR advantage can arise in several ways; for example, SGR, like RGR, can be expressed as the product of net assimilation rate (NAR), specific leaf area (SLA) and leaf mass ratio (LMR) and higher values of any of these components will lead to higher values of SGR. Several studies have demonstrated direct negative correlations between seed size and SLA (e.g. Maranon and Grubb 1993), suggesting a direct link between seed size and leaf construction parameters. However, it is important to remember that these parameters are also size-dependent: for example, a single sheet of ordinary paper can be held rigid by the corner, while the same-sized piece of tissue paper cannot. Thus, small-seeded species, which generally produce seedlings with small leaves, can potentially produce leaves with higher SLA than larger ones. This means that studies hoping to understand interspecific differences in NAR, SLA and LMR also need to correct for size (Rees et. al 2010).

SGR vs RGR

If RGR and SGR are often uncorrelated, which is more appropriate? Clearly the fact that small-seeded plants have a general RGR advantage because of their small size is important when considering the occupation of newly-disturbed habitats, and may indeed contribute to a competition-colonization trade-off (Tilman 1994) or a successional niche (Pacala and Rees 1998) and these in turn could be important coexistence mechanisms. However, if the goal is to understand the mechanisms that underlie differences in individual plant growth rates, then SGR is more revealing. Differences in SGR must be due to differences in its underlying

components (NAR, SLA, LMR) rather than simply a consequence of comparing species of different sizes. Clearly, comparisons could also be carried out at a particular life-history stage if that were of particular interest, however, as species at a similar life-history stage may have very different masses and/or ages, these effects should also be considered in the analysis.

Conclusions

The widespread negative relationship between seed mass and RGR reported in the literature can be generated with no differences in species-specific biology other than differences in seed mass. Hence, SGR needs to be calculated in order to understand whether or not small-seeded species possess additional adaptations for rapid growth. Across our data sets, no such general relationship between seed mass and SGR exists, although our results suggest that life-span could be a useful predictor of the direction of this relationship. The results presented here call for a re-evaluation of the links between seed and seedling traits, plant size and growth rates, which could lead to a significant shift in our understanding of how seed mass and growth rates have co-evolved in different plant communities.

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1 **Figure legends**

2 **Figure 1. The relationship between seed mass and population growth rate in an empty**
3 **landscape**. In A) plants grow exponentially while in B) plant growth is size-dependent
4 (equation 3). Parameter values, $\alpha = 0.8$; $\beta = 0.1$; $T = 10$; and $f = 1$ are estimates taken from
5 growth curves fitted to perennial grasses (Study G). Although the scaling exponent for short-
6 lived species is likely to be higher, the same general curve would apply for any value of $\alpha < 1$.
7 The dotted line in B) shows the population growth rate with a 5% reduction in β, ($\beta = 0.095$).
8
9 **Figure 2 The ten data sets with fitted lines from the linear model.** Studies were grouped
10 according to whether they mostly contained short-lived species (closed circles) or long-lived
11 perennials (open circles). A = genotypes of *Arabidopsis thaliana*, B = European sand-dune
12 annuals, C = Monocarpic perennials 1, D = Monocarpic perennials 2, E = west Asian annual
13 grass species, F = European perennial grass species 1, G = European perennial grass species
14 2, H = C3 and C4 grass species, I = European herbaceous perennial species, J = Bornean
15 Dipterocarp tree species.
16
17
18